

Key principle of the efficient running, swimming, and flying

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Abstract. Empirical observations indicate striking similarities among locomotion in terrestrial animals, birds, and fish, but unifying physical grounds are lacking. When applied to efficient locomotion, the analytical mechanics principle of minimum action yields two patterns of mechanical similarity via two explicit spatiotemporal coherent states. In steady locomotory modes, the slow muscles determining maximal optimum speeds maintain universal intrinsic muscular pressure. Otherwise, maximal speeds are due to constant mass-dependent stiffness of fast muscles generating a uniform force field, exceeding gravitation. Being coherent in displacements, velocities and forces, the body appendages of animals are tuned to natural propagation frequency through the state-dependent elastic muscle moduli.

Key words: variational principle of minimum action (04.20.Fy), locomotion (87.19.ru), biomechanics (87.85.G-).

I. INTRODUCTION

Although evolutionary biologists and comparative zoologists make wonderful generalizations about the movements of terrestrial animals, birds, and fish of different size [1-12], the fundamental physical principles underlying striking similarities in distinct types of movement for organisms remain a challenge [13]. Within the scope of the simplest pendulum model (stiff-legged approximation), it has been demonstrated [14] that humans and other animals, in contrast to human-made engines, accomplish efficient propulsion (maximum power output at minimum power consumption) by tuning musculoskeletal system to the resonant propagation frequency. Storing mechanical energy in elastic oscillations of body parts and in pendulum oscillations of legs or other appendages, animals thereby reduce the energy consumption [1,3], which is minimal at the resonance conditions [14]. In this study, instead of searching for uncovered principles of body mass effects in biology [5], or doing in-depth analysis of equations of motion in pendulum [14], spring [7,8], or vortex [15] approximations and other engineer constructive approaches [9], I address the key principle of mechanics.

In analytical mechanics, the requirement of minimum action between two fixed points of the conceivable trajectory of an arbitrary isolated mechanical system determines Lagrangian $\mathcal{L}(q, v)$, the function of time-dependent coordinates $q(t)$ and instant velocities $v(t) = dq/dt$. The most general property of a freely moving system is spatiotemporal homogeneity implying that the multiplication of \mathcal{L} on an arbitrary constant does not affect the equations of motion, arising from \mathcal{L} . This property, designated as a *mechanical similarity* [16], permits one to establish the major mechanical constraints without consideration of equations of motion. Indeed, following Landau and Lifshitz [16], let us consider the uniform transformation of mechanical trajectories due to linear changing of all coordinates $q \rightarrow aq$ and times $t \rightarrow bt$, and hence velocities $v \rightarrow (a/b)v$, via arbitrary coefficients a and b . Let the potential energy change consequently through a certain exponent s , *i.e.*, $\mathcal{U}(aq) = a^s \mathcal{U}(q)$. Being a quadratic function of velocities, the kinetic energy scales as $\mathcal{K}(av/b) = (a/b)^2 \mathcal{K}(v)$. The requirement of homogeneity of $\mathcal{L}(q, v) = \mathcal{K}(v) - \mathcal{U}(q)$ is self-consistent when both the energies change similar, *i.e.*, $(a/b)^2 = a^s$ or $b = a^{1-s/2}$. Thereby, the frictionless propagation of a classical system obeys the scaling relationships imposed on all principal mechanical characteristics: *period* T , *overall-system speed* V , and *force amplitude* F , namely [16]

$$T \sim t \propto L^{1-s/2}, V \sim v \propto L^{s/2}, \text{ and } F \propto L^{s-1}. \quad (1)$$

The seminal case $s = -1$ introduces Newtonian's intertrajectory coupling force $F \sim M^2 L^{-2}$, where mass M emerges as the dimensional coefficient of proportionality.

It will be demonstrated how the mechanical principle of minimum action applied to musculoskeletal system of animals involved in efficient locomotion may provide basic patterns of biomechanical similarity.

II. MINIMUM ACTION IN BIOMECHANICS

During locomotion, chemical energy released by muscles and mechanical elastic energy stored in body system is transformed into external and internal work and partially lost as a heat. In the case of the off resonance human walking [17], the small velocity-dependent frictional effects were accounted for in the second order of perturbation theory, thereby generalizing the Lagrangian formalism over weakly open systems.

During the muscle forced resonance walking and running (or flying) minimizing energy

consumption, the small damping effects restrict only the amplitude of motion, *i.e.*, *stride length* ΔL (or stroke amplitude) and *muscle length change* ΔL_m , but not the propagation *speed* $V = \Delta L/T$ and *period* T , constrained geometrically [14]. Likewise [17], frictional effects can be therefore neglected in the equations of motion [14], on the first approximation. With the same precision, the principle of mechanical similarity (1) provides

$$T^{-1} = 1/T_{ms} \propto \sqrt{E_{ms}} L_m^{-1}, \quad V \sim V_{ms} \propto \sqrt{E_{ms}},$$

$$F \sim \Delta F \sim F_{ms} \sim \Delta F_{ms} = \varepsilon_m A_m E_{ms}, \text{ with } E_{ms} \propto (L_m)^s \text{ and } g_{ms} \propto (L_m)^{s-1}, \quad (2)$$

when presented in the linear-displacement body ($\Delta L \sim L$) and muscle ($\Delta L_m \sim L_m$) approximation. Introducing in eq. (2) the force change ΔF for the body *force output* F , driving a given animal (of *characteristic length* L , *cross-sectional area* A , and *body mass* M) through the environment, and the effective body rigidity, or longitudinal *stiffness* $K = \Delta F/\Delta L$, one also determines the natural (resonant) *cyclic frequency* $T^{-1} \sim \sqrt{K/M}$ [1,7,8,17,18]. Since the animal locomotion is substantially muscular [1,3,18], the *muscle stiffness* $K_m = E_m A_m/L_m$ (of a muscle of length L_m and cross-sectional area A_m), controlled by the geometry-independent muscle rigidity or *elastic modulus* E_m (ratio of *stress* σ_m to *strain* ε_m , *i.e.*, $(\Delta F_m/A_m)/(\Delta L_m/L_m)$) [7, 18], is also under our consideration. To improve the integrative approach to animal locomotion [1-18] via mechanical [19] and elastic strain [19, 20] similarities, let us determine a muscle-force *field* $g_m \equiv F_m/m$, where the *muscle mass* m (or *motor mass* [6]) is a source of the *active force output* F_m . Furthermore, the scaling relations for physical quantities (shown in eq. (2) by symbol \propto) result from provided relations and constraints imposed by the invariable *body density* $\rho (= M/AL)$ and *muscle density* $\rho_m (m/A_m L_m)$, all common in scaling biomechanics [1,7,9,18].

In this study, the intrinsic muscle modulus E_{ms} , substituting E_m in eq. (2), describes a new dynamic degree of freedom characterizing muscle ability of tuning to the resonance [15] in different locomotory gaits distinguished by the single *dynamic-state exponent* s .

III. RESULTS AND DISCUSSION

The *steady-speed locomotion* for flight mode was first recognized by Hill: "the frequencies of hovering birds are in inverse proportionality to the cube roots of the weights, *i.e.*, to the linear size" [2]. This dynamic regime is pronounced in eq. (2), taken with $s = 0$, by the

propagation frequency $T^{-1} \sim \sqrt{E_{m0}/\rho}L^{-1}$, contrasting with the rigid-pendulum estimate $T_{pend}^{-1} \sim \sqrt{g}L^{-1/2}$ (g is gravitation field) [7,14]. Broadly speaking, Hill's observation plays the role similar to Kepler's observation of third law for planets $T^2 \propto L^3$, following from eq. (1) with $s = -1$.

Hence, when the animal's body travels or cruises slowly for long distances [4] with the constant optimum speed $V_{body}^{(\max)} \sim \sqrt{E_{m0}^{(\max)}/\rho}$, invariant with body weight and frequency, or moves throughout the terrestrial, air, or water environment resisting drag forces, the legs, wings, and tails suggest to maintain constant elastic modulus $E_{m0}^{(\max)}$ in *slow muscles* responsible for the steady locomotion [21]. Consequently, a constant functional intrinsic muscle stress $\varepsilon_m E_{m0}$ is also predicted in eq. (2) with $s = 0$, providing in turn constant safety factor (ratio of muscle strength to peak functional stress), also expected by Hill [2]. These and other relevant constraints of steady-speed locomotion are displayed in table 1.

$s = 0$	Frequency	Length	Speed	Force	Mass
T^{-1}	T^{-1}	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot L^{-1}$	$\rho^{-\frac{1}{4}} E_0^{\frac{1}{4}} \cdot V^{-\frac{1}{2}}$	F^0	$\rho^{-\frac{1}{6}} E_0^{-\frac{1}{2}} \cdot M^{-\frac{1}{3}}$
$\Delta L, L$	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot T$	L	$\rho^{-\frac{1}{4}} E_0^{\frac{1}{4}} \cdot V^{\frac{1}{2}}$	F^0	$\rho^{-\frac{1}{3}} \cdot M^{\frac{1}{3}}$
$V^{(\max)}$	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot T^0$	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot L^0$	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}}$	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot F^0$	$\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot M^0$
$K_{body}^{(\max)}$	$\rho^{\frac{1}{2}} E_0^{\frac{1}{2}} A \cdot T^{-1}$	$E_0 A \cdot L^{-1}$	$\rho^{\frac{1}{4}} E_0^{-\frac{1}{4}} \cdot V^{-\frac{1}{2}}$	$L^{-1} \cdot F$	$\rho^{-\frac{1}{3}} E_0 \cdot M^{\frac{1}{3}}$
$\sigma_{slow}^{(\max)}$	$\varepsilon_m E_0 \cdot T^0$	$\varepsilon_m E_0 \cdot L^0$	$\varepsilon_m E_0 \cdot V^0$	$\varepsilon_m E_0 \cdot F^0$	$\varepsilon_m E_0 \cdot m^0$
$F_{slow}^{(\max)}$	$\varepsilon_m E_0 A_m \cdot T^0$	$\varepsilon_m E_0 A_m \cdot L^0$	$\varepsilon_m E_0 A_m \cdot V^0$	$\varepsilon_m^{(\max)} E_0 A_m$	$\rho_m^{-\frac{2}{3}} \varepsilon_m E_0 \cdot m^{\frac{2}{3}}$

Table 1. Mechanical characteristics of body system and slow individual muscles in the steady-motion dynamic states $s = 0$ prescribed by the principle of minimum muscular action in eq. (2). *Abbreviation:* $E_0 = E_{m0}^{(\max)}$.

The constant maximum propulsive force $F_{body}^{(\max)} \sim E_{m0}^{(\max)} A$, equilibrating all drag forces via slow muscles, *i.e.*, $F_{drag}^{(\max)} \sim F_{slow}^{(\max)}$ shown in table 1, was first documented by Alexander as the peak body force $F_{body}^{(\exp)} \propto M^{2/3}$ [10] exerted on the environment by running, flying, and swimming animals ranged over nine orders of body mass. More recently, the slow-fiber force output $F_{slow}^{(\max)} \propto m^{2/3}$ (table 1) was revealed [6] by statistical regression method in both biological and human-made *slow motors*. The underlying muscle longitudinal field "caused by intrinsic muscle quantity (here associated with E_{m0}), equally stimulated electrically and by the nervous system" [2] decreases linearly with the distance r : $g_{slow}^{(\max)}(r) \approx E_{m0}^{(\max)} \varepsilon_m^{(\max)} / \rho_m r$,

where $\varepsilon_m^{(\max)}$ is nearly isometric strain, as follows from eq. (2) with $s = 0$.

The resonant efficient locomotion broadly prescribes a concerted behavior synchronized in time and coordinated in displacements and forces of the body's appendages. Consequently, the muscle *duty factor* $\beta_m = \Delta t_m/T$, where Δt_m is timing of the muscle lengthening/shortening ΔL_m , is constant, besides the body-mass invariable *Strouhal number* $St = \Delta L/VT$, explaining the tail and wing oscillations in swimmers and flyers [22]. At maximum propulsive efficiency of cruising dolphins, birds, and bats, it was observed as $St_{cruis} \approx 0.3$ [4].

The steady-speed locomotion state also was remarkably established in hovering flying motors via the wing frequencies $1/T^{(\exp)} \propto M^{-1/3}$ [23], as predicted in table 1. However, departures from Hill's findings rationalized here by the dynamic-state exponent $s = 0$ were also debated [24]. For example, it was claimed [7] that Hill's maximal optimum speeds are in sharp disagreement with the peak trot-gallop *crossover speeds* $V_{cross}^{(\exp)}$ measured in quadrupeds [12]. The same could refer to the bipeds [11]. However, as can be seen from the proper empirical data $1/T^{(\exp)} \propto M^{-0.178}$ [11] and $1/T^{(\exp)} \propto V_{cross}^{-1} \propto M^{-0.145}$ [7,12], the measured stride frequencies indicate observations of another kind of mechanical similarity attributed to the *non-steady dynamic state* $s = 1$, prescribed in eq. (2) through the mass-dependent muscle modulus $E_{m1} \propto L_m \propto M^{1/3}$.

The minimum muscle action of legs in fast running rats, wallaby, dog, goat, horse, and human was indirectly revealed through the mechanical similarity derived with the help of *leg spring model* [8], providing the stride frequency $T^{-1} \sim \Delta t_{leg}^{-1} \propto M^{-0.19}$, stride length $\Delta L \propto M^{0.30}$, model-body length $L_{leg} \propto M^{0.34}$, body stiffness $K_{leg}^{(\max)} \propto M^{0.67}$, and body force output $F_{leg}^{(\max)} \propto M^{0.97}$. Relations between the quantities underlying these findings are discussed below and summarized in table 2.

$s = 1$	Frequency	Length	Speed	Force	Mass
T^{-1}	T^{-1}	$g_1^{\frac{1}{2}} \cdot L^{-\frac{1}{2}}$	$g_1 \cdot V^{-1}$	$(\rho g_1^2 A)^{-\frac{1}{2}} \cdot F^{\frac{1}{2}}$	$\rho^{\frac{1}{6}} g_1^{\frac{1}{2}} \cdot M^{-\frac{1}{6}}$
$\Delta L, L$	$g_1 \cdot T^2$	L	$g_1^{-1} \cdot V^2$	$(\rho g_1 A)^{-1} \cdot F$	$\rho^{-\frac{1}{3}} \cdot M^{\frac{1}{3}}$
$V_{cross}^{(max)}$	$g_1 \cdot T$	$g_1^{\frac{1}{2}} \cdot L^{\frac{1}{2}}$	V	$(\rho A)^{-\frac{1}{2}} \cdot F^{\frac{1}{2}}$	$\rho^{-\frac{1}{6}} g_1^{\frac{1}{2}} \cdot M^{\frac{1}{6}}$
$K_{body}^{(max)}$	$\rho g_1 A \cdot T^0$	$\rho g_1 A \cdot L^0$	$\rho g_1 A \cdot V^0$	$\rho g_1 A \cdot F^0$	$\rho^{-\frac{1}{3}} g_1 \cdot M^{\frac{2}{3}}$
$\sigma_{fast}^{(max)}$	$\rho_m g_1^2 \cdot T^2$	$\rho_m g_1 \cdot L_m$	$\rho_m \cdot V^2$	$A_m^{-1} \cdot F_m$	$\rho_m^{\frac{2}{3}} g_1 \cdot m^{\frac{1}{3}}$
$F_{fast}^{(max)}$	$\rho_m g_1^2 A_m \cdot T^2$	$\rho_m g_1 A_m \cdot L$	$\rho_m A_m \cdot V^2$	F_m	$g_1 \cdot m$

Table 2. Mechanical characterization of body of animals and fast muscles in physiologically equivalent non-steady states $s = 1$ prescribed by eq. (2). *Abbreviation:* $g_1 = g_{m1}$.

In accord with table 2, the equilibration of the air drag by wings of flapping birds is manifested by the observed wing frequencies $1/T^{(exp)} \propto M^{-1/6}$ [23]. Moreover, the mechanical similarity between animals resisting air, ground, and water friction forces was demonstrated via the energy cost minimization [9], where the spatiotemporal correlations $V \propto L^{1/2}$ ($\propto M^{1/6}$) were critically explored on *ad hoc* basis.

When the non-steady locomotion conditions associated with the physiologically equivalent (or transient-equilibrium [19]) states $s = 1$ are applied to individual fast-twitch-fiber muscles controlling fast gaits [21], the muscle field is apparently uniform and likely universal [6]. Indeed, the body force field $F_{body}^{(max)}/M \approx 3g$ was first observed via the maximum force output in fast trotting and hopping quadrupeds [8]. Later, mass-specific force output $g_{m1}^{(exp)}$ was empirically established [6] for locomotory individual muscles associated with *fast motors* in running, flying, and swimming animals. One therefore infers that the gravitation field g is not crucial in fast running modes, as proposed in [9]. Moreover, the principle of minimum muscular action suggests that fast muscles may generate force into the whole muscle bulk [25] maintaining constant body stiffness (table 2), unlike the constant pressure characteristic of steady gaits (table 1). In other words, the fast muscles are not simple passive springs [3,26], attributed to $s = 2$ and having length-independent period, but are complex systems being able to activate fibres in both parallel and series. Maintaining the uniform muscle force field g_{m1} , the *Froude number* ($Fr = V/\sqrt{gL}$ [1]) must be mass-invariable, for both muscle system ($Fr_{fast} \sim \sqrt{g_{m1}/g}$) and body system, apart from the corresponding Strouhal number. For fast running gaits in mammals, $Fr_{run}^{(exp)} \approx 1.5$ and $St_{run}^{(exp)} \approx 0.4$ [8].

IV. CONCLUSION

The main goal of this letter is to demonstrate how the complex biological phenomenon of mechanical similarity in animal locomotion allows to be rationalized and formulated as a predictive, quantitative framework. It has been shown how the fundamental physical principle of minimum action applied to locomotory muscles via intrinsic elastic moduli quantifies amazing similarities established empirically between maximal speeds, frequencies, forces, and other relevant mechanical characteristics of animals locomoting in a certain gait. Naturally operating the softness of legs, wings, and tails, the efficient runners, flyers, and swimmers are shown to maintain constant Strouhal number via the universal constant muscle pressure, when traveling or cruising at steady speeds. When acting quickly at higher speeds, escaping from predators, or when hunting, the successful runners, flyers, and swimmers appear to maintain the universal field in the whole bulk of fast muscles, at least at crossover speeds. This uniform field eventually results in the bodyweight depending, fixed muscle stiffness and universal Froude and Strouhal numbers. The provided from first principles study illuminates and supplements a wide spectrum of reliable empirical findings in walking and running bipeds [3,11], trotting and galloping quadrupeds [6-9,12]; hovering and flapping birds [2-4,10,11], bats, and insects [3,4,9]; undulating and tail-beating fish [2-4,9,10], dolphins [2,4], sharks [4], and whales [2].

On the other hand, the study of muscle characteristics, including obtained scaling relations to muscle and body mass, is limited by the linear-displacement muscle approximation. It can be shown however that the top speeds attributed to limiting animal performance [19,24] cannot be achieved by the linear-strain elastic muscle fields. The consequences of application of the minimum action to specific fast locomotory muscles structurally adapted to a certain mechanical activity, such as motor, brake, or strut functions [3] prescribed by non-linear elastic effects [25] will be discussed elsewhere.

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